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The Migration of Nervous Elements into the Dorsal and Ventral Nerve-Roots of Embryos of the Pig

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THE MIGRATION OF NERVOUS ELEMENTS INTO THE DORSAL AND VENTRAL NERVE-ROOTS OF EMBRYOS OF THE PIG.*

BY ALBERT KUNTZ.

With two Figures.

That nervous elements migrate peripherally from the neural tube, during early embryonic development, has been observed by several investigators. Harrison ('01) called attention to medullary cells migrating into the ventral nerve-roots of embryos of the salmon. Bardeen ('03) observed that "in mammals, as well as in the lower vertebrates, a certain number of cells wander out from the spinal ganglia and cord along with the bundles of axis-cylinder processes." In his work on embryos of the chick, Carpenter ('06) has shown that cells of an indifferent character migrate from the ventral wall of the mid-brain along the oculomotor nerve and become transformed into nerve cells of the ciliary ganglion. In a more recent paper Carpenter and Main ('07) have described the migration of medullary cells into the ventral nerve-roots of embryos of the pig.

In his study of the earliest differentiations in the central nervous system, Schaper ('97) has shown that the germ cells (Keinzellen) of His cells of epiblastic origin undergoing mitotic division near the internal limiting membrane of the medullary tube—give rise to cells which he characterizes as indifferent, which migrate toward the mantle layer and are there transformed either into neuroblasts or into embryonic supporting cells. In the higher vertebrates some of these indifferent cells undergo further division by mitosis in the mantle layer, thus giving rise to other indifferent cells after having migrated from their original position.

In the cells which Carpenter and Main observed migrating into the ventral nerve-roots of embryos of the pig, they have recognized the indifferent cells of Schaper.

In studying embryos of the pig for the purpose of tracing the development of the sympathetic nervous system, the writer has observed medullary cells migrating into both ventral and dorsal nerve-roots. In transverse sections of embryos of the pig from 9 to 13 mm. in length, breaches of considerable extent in the external limiting membrane of the medullary tube may be observed in the region of the ventral nerve-roots. Among the fibers of the nerve-roots passing through these breaches cells may be observed migrating out from the neural tube (fig. I). I have been able to substantiate the observation of Carpenter and Main that cells may be found "just inside the external limiting membrane, in an intermediate position half in and half out of the neural tube, and in the base of the nerve-root just outside the external limiting membrane."

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Among these migrating cells I also recognize, as did they, the indifferent cells of Schaper. In several sections, however, cells with large rounded or elongated nuclei and cytoplasm drawn out to a point at one side were observed among the fibers of the ventral nerve-root, migrating with the indifferent cells. In these cells I recognize the neuroblasts of Schaper. They are much fewer in number than the indifferent cells but are distributed indiscriminately among them. When observed in the spinal nerve-roots the tapering end is usually directed peripherally. This, also, is in accordance with the usual position of the neuroblasts in the mantle layer. The orientation of the cells in the neural tube is such that two general courses of migration into the ventral nerve-root may be recognized; the one directly outward from the ventral zone; the other ventro-laterally toward the base of the nerve-root, from the region in which later the lateral horn of the gray matter arises.

In transverse sections of embryos of the pig 6 and 7 mm. long, breaches in the external limiting membrane of the neural tube occur quite frequently in the region of the dorsal nerve-root. Through these breaches medullary cells migrate so freely that in many sections lines of cells practically touching each other end to end can be traced from the mantle layer into the proximal part of the dorsal nerve-root (fig. II). Further evidence for the migration of medullary cells into the dorsal nerve-roots is seen in the fact that in many sections of embryos 6 and 7 mm. long, where no breaches occur, cells are found in contact with the external limiting membrane in the region of the dorsal nerve-root. In embryos 9 mm. and over in length this area, as shown in fig. I, is always occupied by fibers of the dorsal nerve-root, and rarely are cells found among them. Two general courses of migration may also be recognized in the dorsal region. One of these courses has its origin in the dorsal zone. Some of its cells move in a slight curve directly toward the dorsal nerve-root, others pass from the most dorsal region along the inner surface of the external limiting membrane. The other course tends dorso-laterally from regions ventral to the dorsal nerve-root. The cells of the latter course probably originate in the same region as those which move ventro-laterally toward the ventral nerve-root.

Among the cells migrating into the dorsal nerve-roots, I recognize both the "indifferent cells" and the "neuroblasts" of Schaper.

My observations do not permit me to conclude how early the first migration of cells from the neural tube takes place. In studying a very young embryo in which, however, the external limiting membrane was completely formed, no migrating cells could be observed. It is probable, therefore, that cells do not migrate out of the neural tube until the fibers of the nerve-roots have penetrated the external limiting membrane.

As observed above, cells are rarely found among the fibers of the dorsal nerve-root near the external limiting membrane inside the neural tube, in embryos 9 mm. and over in length. Migration into the dorsal nerve-root probably ceases before a length of 9 mm. is reached. Migration into the ventral nerve-root continues longer and seems to be most active in embryos from 10 to 13 mm. in length. In embryos over 13 mm. in length migration is rarely observed and probably does not continue far beyond that stage.

There are four points to which the writer wishes to call special attention in this paper. (1) Medullary cells migrate into both dorsal and ventral nerve-roots. (2) These migrating cells seem to have their origin in more or less

definite regions in the neural tube. (3) Migration from the neural tube seems to be limited to a comparatively short period during embryonic development. (4) While the majority of the cells which migrate into the dorsal and ventral nerve-roots are cells of an indifferent character, cells may be recognized among them, which are to be regarded as the neuroblasts of Schaper.

These observations give rise to an important question. What is the destiny of those cells which migrate from the neural tube into the dorsal and ventral nerve roots? This question the writer hopes to consider more fully in a later paper. But, as the way has been opened for a priori speculation a few suggestions may be ventured here.

Harrison ('01) has already suggested the possibility that the medullary cells which he saw migrating into the ventral nerve-roots of embryos of the salmon may wander farther peripherally, i. e., into the sympathetic ganglia, and there give rise to sympathetic motor neurones. Bardeen ('03) suggests that the cells which wander out from the spinal ganglia and cord along with the bundles of axis-cylinder processes of the nerve-roots may take some part in the formation of the neurilemma, but believes with Vignal and Gurwitsch that in mammals the cells composing the neurilemma arise largely from mesenchyme. Harrison's experimental observations on the tadpole ('06) seem to prove that some of the elongated cells found among the fibers of developing nerves, which become cells of the neurilemma, are derived from spinal ganglia. Carpenter and Main ('07) "feel sure" that some of the medullary cells which escape from the neural tube become cells of the neurilemma, and there subserve a supporting function similar to that of the neuroglia cells in the central nervous system.

Thus far only cells of an indifferent character have been considered. May not the fact that neuroblasts migrate with the indifferent cells into both dorsal and ventral nerve-roots shed some new light on the entire problem? To trace these cells to their ultimate destination is a matter of extreme difficulty, if not impossibility, with the aid of present staining methods alone. In the light of Schaper's researches, however, we must conclude that the neuroblasts which migrate into the dorsal and ventral nerve-roots have already undergone differentation and must develop into neurones. Having once passed beyond the borders of the neural tube they must migrate farther peripherally. Nothing seems more probable, therefore, than that they should wander along the visceral ramus and give rise to neurones in the sympathetic ganglia. Any conclusion, however, on this point would at present be hasty. We feel that these migrant cells, both the "indifferent cells" and the "neuroblasts" of Schaper, are fraught with great potentialities and invite the most careful scrutiny into their fate.

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EXPLANATION OF FIGURES.

Fib. I. Transverse section of neural tube and spinal ganglion of a 12 mm. embryo of the pig. XI65.
dnr—dorsal nerve root. spg—spinal ganglion. nb—neuroblast. vnr—ventral nerve-root. ic—indifferent cells.

Fig. II. Transverse section of neural tube and spinal ganglion of a 6 mm. embryo of the pig. XI65.
ic—indifferent cells. dnr—dorsal nerve-root. nb—neuroblast. spg—spinal ganglion.